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SUBTLE DIFFERENCES BETWEEN MALE AND FEMALE OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* IN FEEDING ON THE BIVALVE *MACOMA BALTHICA*

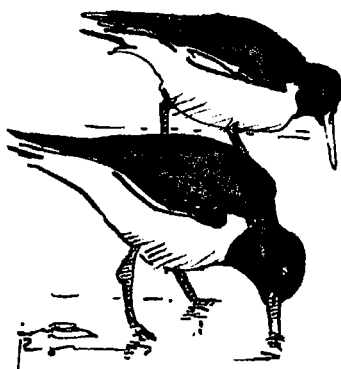
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& DICK HEG¹

Hulscher J.B., D. Alting, E.J. Bunscocke, B.J. Ens & D. Heg 1996. Subtle differences between male and female Oystercatcher *Haematopus ostralegus* feeding on the bivalve *Macoma balthica*. *Ardea* 84A: 117-130.

In this paper an analysis is made of subtle behavioural differences between adult male and female Oystercatchers feeding on *Macoma balthica* under field conditions and in captivity. *Macoma* is a tellinid bivalve that in the Dutch Wadden Sea is mainly preyed upon during spring and summer when it is buried at a shallow depth. ♂♂ lift *Macoma* more, whereas ♀♀ handle them mostly *in situ*. Both sexes handle a *Macoma in situ* faster than one lifted. Time loss of ♂♂ in handling more lifted *Macoma* is compensated by the larger size of lifted *Macoma*, which yields more flesh. The time the birds need to find an edible *Macoma* is similar for both sexes, resulting in equal mean food intake rates for ♂♂ and ♀♀ in the field. Lifted *Macoma* are generally hammered and, since ♂♂ with their short strong bills are more likely to hammer bivalves than ♀♀, this difference in bill morphology might explain why ♂♂ more often lift *Macoma* than do ♀♀, especially as hammering produces a blunt bill tip which would reduce efficiency at opening *Macoma in situ*. However, none of the selected bill morphology variables showed a relationship within the sexes that explained the differences between the sexes.

Key words: Oystercatcher - *Haematopus ostralegus* - bill morphology - prey profitability - *Macoma balthica*

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INTRODUCTION

In tidal areas Oystercatchers predominantly feed on bivalves and worms (Hulscher 1996). Although prey choice broadly overlaps between the sexes, there is some differentiation: ♀♀ more often prey on deeply buried prey, like clams and worms, while ♂♂ are more likely to take heavily armoured large prey that live on or just beneath the surface, such as Mussels *Mytilus edulis* and Cockles *Cerastoderma edule*. These differences in prey choice are related to differences in bill morphology: ♀♀ have long and thin bills with

pointed tips, while ♂♂ have short and thick bills, often with blunt tips (Hulscher & Ens 1992, Durell *et al.* 1993). This association suggests that structural features of the bill predispose the individual to feed on a particular prey in a particular manner, with the subsequent adaptive modification of the shape of the bill tip then reinforcing this prey choice (see review by Sutherland *et al.* 1996). Clearly, the Oystercatcher bill is a complex trait and the existence of subtle differences between ♂♂ and ♀♀ may provide an opportunity to study the constraints that shape such a character during evolution. For instance, Hulscher & Ens (1992) sug-

gest that there is a trade-off between increasing bill length, which helps birds reach deeply buried prey, and bill strength, which helps them to break into heavily armoured prey.

In this paper we examine whether the sex differences in bill morphology result in differences in feeding tactics when male and female Oystercatchers simultaneously feed on *Macoma balthica* in the same area. *Macoma* is a small tellinid bivalve, up to 24 mm shell length. It is very common in the littoral community of sandy and muddy estuaries (Beukema 1976) and is an important prey species for Oystercatchers (Hulscher 1982). In summer, most *Macoma* are buried about 20 to 30 mm deep in the sediment, while in winter they are found a little deeper, at 40 to 50 mm (Zwarts & Wanink 1989, 1993). Thus, *Macoma* is nearly always within reach of both ♂♂ and ♀♀, but its profitability could depend on burying depth, as in *Scrobicularia plana* (Wanink & Zwarts 1985). Hence, bill length might be important for efficient consumption of this prey. Similarly, shell thickness of *Macoma* is comparable to the shell thickness of Cockles and Mussels, indicating that bill strength might also be important. After describing the differences in the behaviour of ♂♂ and ♀♀ when feeding on this prey, we investigate which, if any, of the morphological variables may explain them.

STUDY AREA AND METHODS

Free-living birds

Oystercatchers were trapped in the Dutch Wadden Sea on the nest in May-June on the island of Schiermonnikoog and by nest-trapping or by cannon- and mist-netting throughout the year at Paesens along the coast (Fig. 1). The birds were individually marked with colour rings and the following measurements taken: body weight (g), wing length (maximum cord, mm), bill length from the feather margin to the tip, bill height at the deepest point, i.e. at the proximal end of the gonys, about half way the length of the bill and bill tip width at 3 mm from the tip (per 0.1 mm).

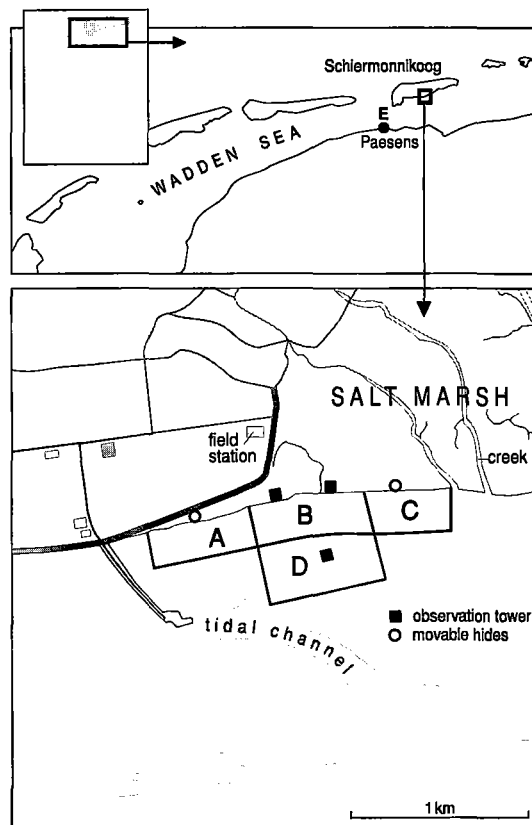


Fig. 1. The two localities in the Dutch Wadden Sea where the Oystercatchers were studied: Paesens along the coast and the island of Schiermonnikoog. The feeding areas consisted of sandy mudflats, at Paesens about 300 m down shore, at Schiermonnikoog at distances varying between 10-800 m from the shore line.

Bill tip shape, in lateral view, was categorized as pointed, intermediate and blunt. In a smaller sample of birds, the height of the bill at a point 3 mm from the tip was also measured (Swennen *et al.* 1983, Hulscher & Ens 1992, Durell *et al.* 1993).

Observations were done in late spring and summer and were restricted to marked adult birds of known sex, as determined from copulations or biometrics (Zwarts *et al.* 1996). Observations were made with 40-60× telescopes from towers, 4-6 m high, at distances from 10 to 300 m and registered with event recorders. Prey were iden-

tified visually. After an Oystercatcher detects a *Macoma* in the sediment by contacting the shell with the bill tip, it opens it in either of two ways: directly in the sediment beneath the surface (*in situ*), or on the mud surface, after it has lifted the bivalve from the substrate, pinching it between the mandibles (lifting). Handling time was measured from the moment the bird started manipulating the prey until the last piece of flesh had been removed and swallowed.

The size of the morsels of flesh extracted per prey (bite size) was estimated on a 5 point scale, using the 10 mm high colour ring as reference. Using calibration experiments with morsels that were subsequently burned, these field estimates could be transformed to ash free dry weights (AFDW). This enabled the calculation of the food intake of the birds (Kersten & Brenninkmeijer 1995). The shape of the bill tip, in lateral view, (pointed, intermediate or blunt) of the feeding birds was noted.

The data were obtained from six series of observations. They mainly differ in the number of feeding parameters registered:

Series 1: Paesens, area E (Fig.1), 300 m down shore from the salt marsh, May 1979; birds feeding exclusively on *Macoma* were selected and observed for 10 minutes; handling times of *Macoma* opened *in situ* or after lifting, along with the total searching time per observation period, were registered.

Series 2: Schiermonnikoog, areas B+D, March-August 1986-1989; randomly chosen feeding individuals were observed for a while, usually lasting through 2-10 prey captures. Total feeding time, number of prey captures and the species were registered. All observations from a single individual obtained over the years were pooled. Only individuals with in total 20 or more prey captures were included.

Series 3: Schiermonnikoog, area B, April-August 1986; paired ♂♂ and ♀♀ feeding together in the territory, were observed for long periods (often complete low water periods) throughout the breeding season. Handling times, bite sizes and the length of searching bouts between prey

captures were registered. Observations from each individual were pooled over the whole season.

Series 4: Schiermonnikoog, area B+C, May 1992; matched observations of paired ♂♂ and ♀♀ feeding in the territory were made for a varying length of time. Number of prey consumed and total foraging time were registered. Data from an individual were pooled. Only birds with 20 or more prey captures are included.

Series 5: Schiermonnikoog, area A, May 1993; as series 4, with the addition of handling times and accompanying bite sizes for each prey capture and of searching times between prey captures.

Series 6: Schiermonnikoog, area A+B+C, March-August 1993; male and female birds were observed for a period of usually 20 prey captures throughout the season. Total number and biomass (AFDW) of eaten prey per species in monthly periods were pooled over all male and female observations.

Experiments in captivity

A male (bill length 74.0 mm) and female (bill length 79.2 mm) Oystercatcher caught on the nest at Schiermonnikoog were adjusted to captivity in an outdoor cage at the field station. Seven containers (60×35×12 cm) filled with sieved sediment from the local mudflats were stocked with a varying number of *Macoma* of a single size class: 14, 15, 16, 17, 18, 19 or > 20 mm shell length. *Macoma* collected from the local flats were allowed to bury themselves for 24 hours before observations began. Burying depth and fresh meat weight of the *Macoma* were determined by slicing 2 cm thick layers of sediment in control containers after a settling period of 24 hours.

Four containers were offered to the Oystercatchers simultaneously. In each session, the birds were allowed to feed in turn, switching the sequence between sessions, for a varying length of time. Before observations began on a new bird, the emptied shells were removed and the surface of the sediment smoothed in order to remove possible surface marks. This ensured that the feeding circumstances for the two birds were comparable.

Handling times and bite sizes were recorded from a hide at a distance of 2 m. Total searching time per session was determined. The depth to which the bill penetrated into the sediment at the moment the bird found a *Macoma* and started to open it (finding depth) was also noted.

Statistical analysis

Results from each captive bird were pooled for all sessions and averaged. When comparing the sexes in an analysis of the field observations, the results of the different series are not pooled, but are presented separately, to allow for differences in conditions between areas and/or years. In contrast, all data were pooled when analysing whether differences in bill morphology could explain the differences between the sexes. For each morphological variable, we first tested whether there was a significant interaction with sex, using ANCOVA for continuous morphological variables and two-way ANOVA for categorical morphological variables. If there was no interaction, the contribution of sex and morphology was then assessed with ANCOVA or ANOVA using the regression approach, i.e. the contribution of each factor or covariate was assessed, after controlling for all others. For all analyses the fraction lifted was arcsine transformed. Statistical analyses were performed using SPSS PC⁺ (Norušis/SPSS Inc. 1992).

RESULTS

Importance of *Macoma* in the diet

We shall first investigate to what extent *Macoma* contributes to the summer diet and whether ♂♂ and ♀♀ differ in this respect. At Paesens, *Macoma* is an important staple food. However, the precise contribution of *Macoma* to the diet of the population as a whole cannot be calculated, because only individuals feeding solely on *Macoma* were selected for observations. On Schiermonnikoog, all prey captures were identified in all observation series (Table 1). Here, *Macoma* forms a substantial part of the summer diet, but

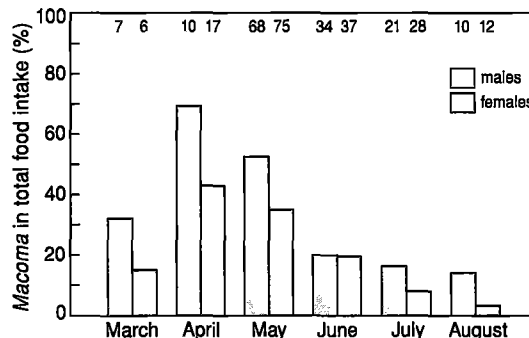


Fig. 2. The mean monthly percentages of *Macoma* in the total food intake (AFDW) of ♂ and ♀ Oystercatchers during the breeding season on Schiermonnikoog (series 6). Figures on top of the bars refer to the number of observations lasting for periods of 20 prey captures or more. The share of *Macoma* in the diet of ♂♂ over the whole season surpassed that of ♀♀ (Mann-Whitney *U*-test; $U = 10568.0$, $n_1 = 150$, $n_2 = 171$, $p = 0.0021$).

♂♂ always took more *Macoma* than ♀♀. In four of the five series, these differences were significant. The relative importance of *Macoma* in the total biomass intake of both sexes steadily declines over the season from April onwards (as illustrated with data series 6 in Fig. 2). A similar trend is reported by Bunschoke *et al.* (1996) for data series 2 and 3; the other three data sets only apply to one month (i.e. May).

Feeding behaviour

Field observations The next step is to determine whether, and in which aspects, ♂♂ and ♀♀ differ in feeding procedures when feeding on *Macoma*. How do their handling and handling times compare and do these affect profitability and intake rates? ♂♂ always lift *Macoma* significantly more than ♀♀ (Fig. 3A). Both sexes handle *Macoma in situ* much faster than when lifting them (Fig. 3B), but sexual differences within categories of handling are small and not consistent.

In series 3 and 5, where bite sizes were registered, ♂♂ and ♀♀ extracted more meat from a *Macoma* opened after lifting than from one opened *in situ* (Fig. 3C). Since the size of the shells

Table 1. Percentage *Macoma* in the diet, based on the total number of eaten prey, of adult ♂ and ♀ Oystercatchers at Schiermonnikoog; *n* = number of birds, each with 20 prey at least in the diet. Inter-sexual differences were tested with the Student-*t* test.

Series	♂			♀			<i>t</i>	<i>p</i>
	\bar{x}	<i>SD</i>	<i>n</i>	\bar{x}	<i>SD</i>	<i>n</i>		
2	53.70	20.71	71	37.49	23.87	78	4.41	< 0.001
3	65.53	34.49	18	38.73	33.05	16	2.31	< 0.028
4	42.80	31.25	31	20.74	25.42	34	3.13	< 0.005
5	59.06	28.85	14	48.35	32.90	16	0.34	> 0.750
6	53.19	29.50	52	43.23	24.42	57	1.93	< 0.05

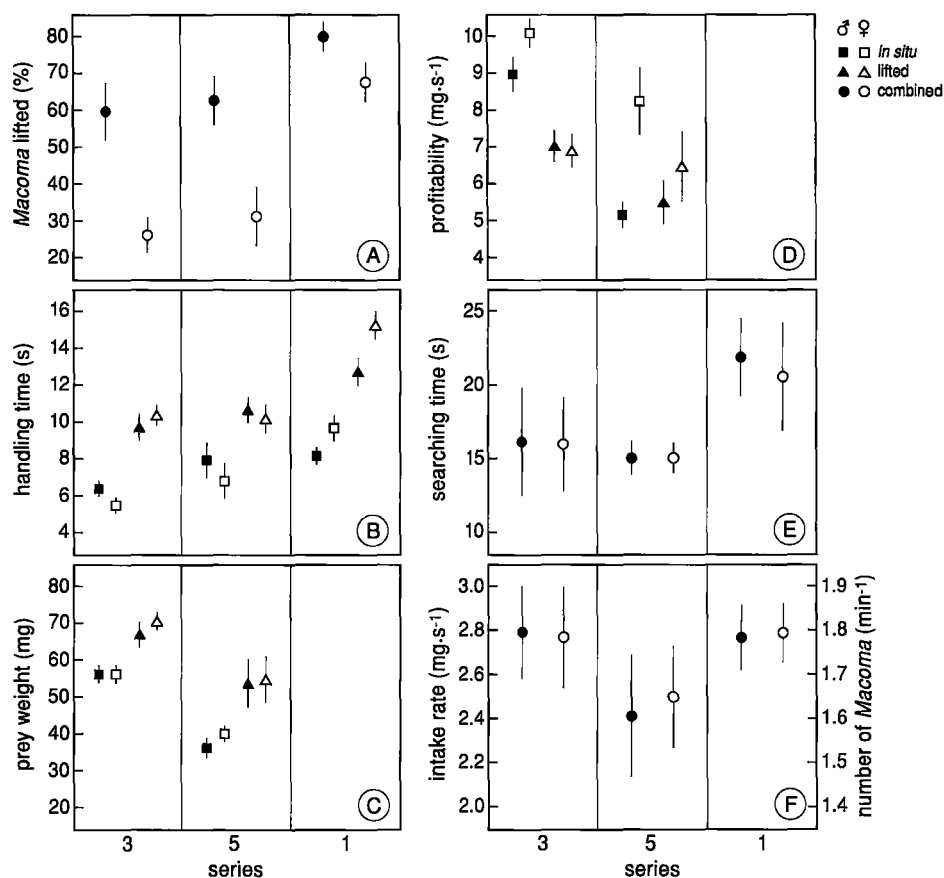


Fig. 3. Different feeding parameters (means \pm SE) for free-living adult Oystercatchers feeding on *Macoma* at Paesens (series 1) and Schiermonnikoog (series 3 and 5). ♂ ♂: closed symbols; ♀ ♀: open symbols. (A) The percentage of *Macoma* eaten which were lifted. (B) Handling time per *Macoma* eaten: the time spent in opening and cleaning *in situ* (squares) or lifted (triangles). (C) The quantity of flesh extracted from a *Macoma in situ* (squares) or lifted (triangles). (D) The profitability of handling *Macoma* eaten *in situ* (squares) or when lifted (triangles). (E) Searching time per *Macoma* eaten (*in situ* and lifted *Macoma* combined). (F) Intake rate per time feeding: for series 3 and 5 in mg AFDW s⁻¹ (left axis), for series 1 in number of *Macoma* eaten min⁻¹ (right axis).

from which the flesh was extracted could not be determined in the field, we do not know whether the size of the shell, the wet weight of the flesh of the prey, and the precision of the cleaning process by the birds are the same or different when prey are opened *in situ* or after lifting.

The profitability of handling *Macoma in situ* is generally greater than that of lifting (Fig. 3D), though the difference is not always significant. There are no apparent inter-sexual differences in the profitability of handling lifted *Macoma*. However, ♀♀ do significantly better in handling *Macoma in situ* than ♂♂.

On Schiermonnikoog, the major other staple food close to the shore was *Nereis diversicolor*, but individual Oystercatchers usually took only one prey type for long periods. According to Ens *et al.* (1996) this is due to incompatibilities in the

hunting technique required to exploit different prey types. In such a situation, the total fraction of the feeding time spent in searching during a feeding bout where predominantly one species was caught may be considered as searching time for that particular prey species. In series 1 the birds exclusively fed on *Macoma*. This was not so in series 3 and 5, and only searching bouts preceding *Macoma* captures were selected and summarized. No differences in searching times between the sexes are apparent (Fig. 3E).

The availability of bite size measurements in series 3 and 5 allow intake rate to be calculated. No differences between the sexes were found in either series (Fig. 3F). Only the number of *Macoma* consumed was noted in series 1, and no difference between the sexes was found in that series either.

Table 2. Summary of the overall results of the male (White) and female (Yellow) Oystercatcher when feeding on *Macoma* in captivity; *n* = the number of *Macoma* eaten. The mean profitability (mg s^{-1}) of handling *Macoma in situ* or when lifting respectively, is calculated by dividing the means of the meat extracted by the time needed to handle such a *Macoma*. The mean intake rate (mg s^{-1}) was calculated by dividing the total amount of meat ingested by the total time spent in feeding (searching+handling) over the whole length of the feeding experiment. Differences were tested with the Student-*t* test. Intra-sexual comparison of the size of the *Macoma* eaten *in situ* and lifted revealed for the ♂ $t = 12.90$, $p < 0.001$ and for the ♀ $t = 1.80$, $p < 0.05$; of the handling times per *Macoma in situ* against lifted for the ♂ $t = 11.58$, $p < 0.001$ and for the ♀ $t = 12.30$, $p < 0.001$; of the quantity of meat extracted per *Macoma in situ* against lifted for the ♂ $t = 12.30$, $p < 0.001$ and for the ♀ $t = 5.29$, $p < 0.001$.

		♂ (White)			♀ (Yellow)			<i>t</i>	<i>p</i>
		\bar{x}	<i>SD</i>	<i>n</i>	\bar{x}	<i>SD</i>	<i>n</i>		
<i>Macoma</i> lifted, %			38.3			8.1			
Size eaten	<i>in situ</i>	15.97	1.44	240	16.44	1.70	513	3.71	<0.001
<i>Macoma</i> , mm	lifted	17.97	1.20	149	16.91	1.66	45	4.72	<0.001
Handling time,	<i>in situ</i>	8.90	4.61	240	6.39	2.66	513	9.43	<0.001
s per <i>Macoma</i>	lifted	15.49	6.60	149	12.16	5.72	45	3.05	<0.001
Meat extracted,	<i>in situ</i>	62.77	15.58	240	64.59	14.91	513	1.54	<0.100
mg <i>Macoma</i>	lifted	80.29	11.97	149	76.52	8.70	45	1.96	0.025
Profitability,	<i>in situ</i>	7.05			10.11				
mg s^{-1} handling	lifted	5.18			6.29				
Searching time, s			14.50			12.86			
Intake rate, mg s^{-1}			2.67			3.31			

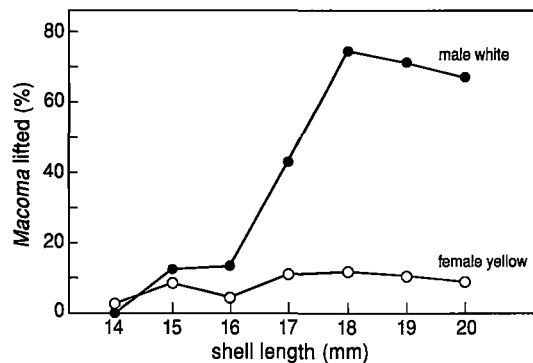


Fig. 4. The percentage of lifted *Macoma* in relation to shell length, for the male (White) and female (Yellow) Oystercatcher during the feeding experiment. For the ♂ the class means (y , %) were positively correlated with shell length (L , mm): $y = -189.8 + 13.53 \times L$, $r = 0.928$, $p < 0.005$, $n = 7$; not for the ♀: $r = 0.510$, $p > 0.1$, $n = 7$.

Experiments in captivity The results from the two captive birds (Table 2) agree in most aspects with those of the free-living birds. The ♂ lifted *Macoma* more often than the ♀. Both, ♂ and ♀ needed more time to handle a lifted *Macoma* than one *in situ*. They also extracted more meat from a lifted *Macoma* but handled *Macoma in situ* more profitably than lifted ones. However, although the feeding conditions for the two birds were the same, the intake rate of the ♀ was much higher (24%): she searched for *Macoma* at a higher rate, opened more *Macoma in situ* and handled specimens both *in situ* and when lifted much faster than the ♂.

As the captive birds fed on *Macoma* of different size classes, three additional aspects of feeding behaviour could be explored. First, both birds lifted more *Macoma* as shell length increased; this effect was significant for the ♂, not for the ♀ (Fig. 4). Second, both birds found the *Macoma* they opened *in situ* at a smaller depth than those they lifted (Fig. 5A). However, no relationship was found between finding depth and shell length in either handling category. This is rather surprising, since the mean burying depth of *Macoma* retrieved after 24 hours of settling was negatively

correlated with shell length (Fig. 6), as previously shown by Hulscher (1973). Third, both birds extracted more flesh from a lifted *Macoma* than from one of corresponding size taken *in situ* (Fig. 5B). This makes sense, because the deeper a *Macoma* of a certain size was buried the greater was its weight in flesh (Fig. 7), analogous to the situation in the field (Zwarts & Wanink 1991).

Conclusions The results indicate that the intake rates of ♂♂ and ♀♀ hardly differ in the field (Fig. 3F), but they are achieved in different ways. Searching time is similar for ♂♂ and ♀♀ (Fig. 3E). The ♂♂ lift *Macoma* significantly more than the ♀♀ (Fig. 3A) and the ♀♀ take more *Macoma in situ*. A lifted *Macoma* yields more flesh, on average, than a *Macoma* taken *in situ* (Fig. 3C). Although this presumably benefits the yield in ♂♂, lifting prey requires more handling time (Fig. 3B) than eating them *in situ*, thus reducing the advantage. The net effect is that, despite the differences between the sexes in the method of taking *Macoma* (by lifting or *in situ*), their intake rates are rather similar.

Morphology of the bill

Why are the feeding procedures of the ♂♂ and ♀♀ dissimilar? Bill length and bill depth and the width and shape of the bill tip differ between the sexes (Table 3). If these differences in bill morphology cause the difference in handling of *Macoma* between the sexes, there should neither be a significant interaction between sex and the particular bill feature, nor should sex have an independent effect after the bill feature of interest has been controlled for. Below, we shall test this expectation for each bill feature, after giving some *a priori* considerations on the most likely relationship. After a *Macoma* is located the shell must be opened and the flesh loosened and swallowed. The shape and dimensions of the bill tip in relation to the width of the gape of the *Macoma*, and the depth at which it must be opened and cleaned in relation to the bill length may both be of importance.

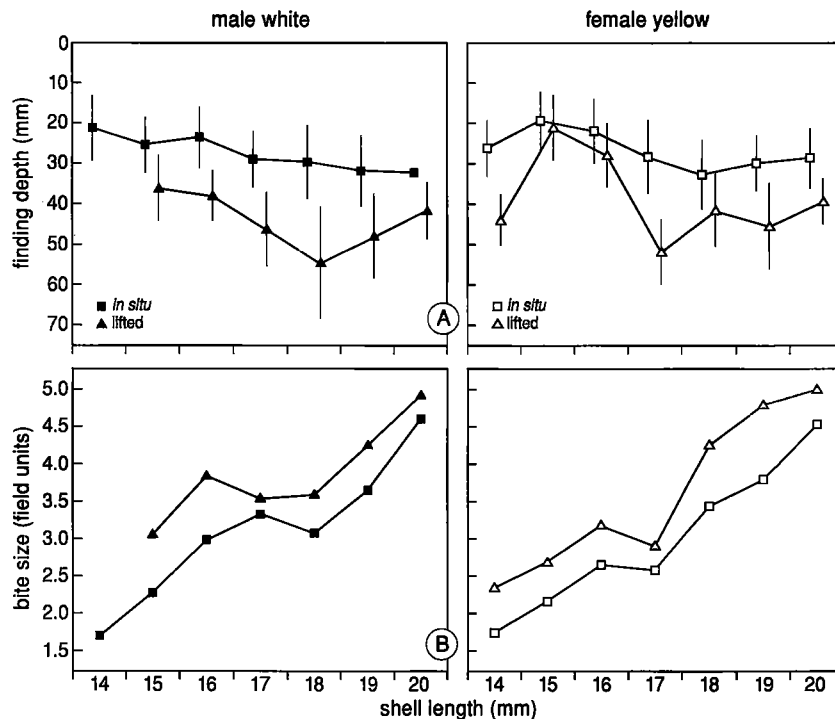


Fig. 5. (A) Finding depth (mean \pm SD) of *Macoma* opened *in situ* or after lifting in relation to shell length, of the male (White) and female (Yellow) Oystercatcher during the feeding experiment. A two-way analysis of variance on the depth averages revealed that the difference in depth between *Macoma* eaten *in situ* or when lifted was highly significant in the σ ($R^2 = 0.708$, $p < 0.001$) and φ ($R^2 = 0.488$, $p < 0.001$), but shell length was less important ($R^2 = 0.177$, $p > 0.25$ in the σ and $R^2 = 0.370$, $p < 0.25$ in the φ). (B) Relation between the mean bite size and shell length of *Macoma* either handled *in situ* or lifted, of the male (White) and female (Yellow) Oystercatcher during the feeding experiment. A two-way ANOVA showed that both birds took significant bigger bite sizes from *Macoma* of larger size (σ $R^2 = 0.826$, $p < 0.010$; φ $R^2 = 0.882$, $p < 0.001$) and also from lifted than from *in situ* *Macoma* (σ $R^2 = 0.130$, $p < 0.005$; φ $R^2 = 0.102$, $p < 0.001$).

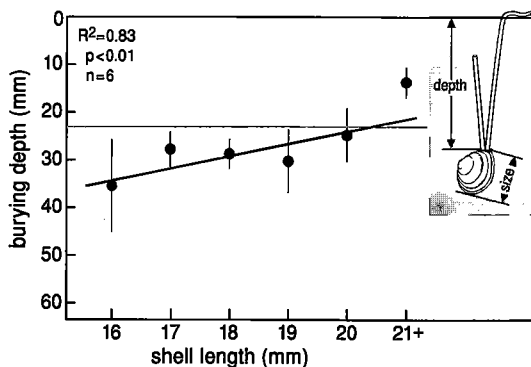


Fig. 6. Burying depth (mean \pm SE) of *Macoma* of different shell length after 24 hours of settling in containers with sediment as used in the experimental set-up with the captive birds. Burying depth (means of shell length classes: y , mm) was negatively correlated with shell length (L , mm): $y = 83.03 - 3.03L$; $r = 0.912$, $p < 0.01$. The broken line indicates the mean burying depths of *Macoma* of corresponding sizes during the summer in the field (Zwarts & Wanink 1989).

Table 3. Sexual dimorphism of bill characteristics of adult Oystercatchers of Schiermonnikoog during the breeding season, May-June; measurements in mm, n = number of birds. Differences between ♂♂ and ♀♀ were tested with the Student- t test.

	♂♂			♀♀			t	p
	\bar{x}	SD	n	\bar{x}	SD	n		
Bill length	69.8	3.12	679	78.4	3.78	639	45.4	< 0.001
Bill depth	10.6	0.46	674	10.2	0.43	638	17.28	< 0.001
Width of bill tip:								
pointed	1.28	0.17	25	1.25	0.17	175	1.01	< 0.329
intermediate	1.25	0.19	220	1.34	0.20	354	4.13	< 0.001
blunt	1.35	0.23	430	1.44	0.23	107	3.86	< 0.001
all shapes	1.32	0.22	676	1.25	0.21	637	1.16	< 0.248
Depth of bill tip								
all shapes	5.03	0.51	63	4.18	0.65	57	8.00	< 0.001

Table 4. What are the effects of sex and bill length on parameters of handling *Macoma*? Each row provides the results for one parameter. Variance explained in an ANCOVA with separate slopes (R^2-i = interaction) and an ANCOVA with fixed common slope (R^2-l and R^2-s = bill length and sex). Stars indicate statistical significance: * p < 0.05, ** p < 0.01, *** p < 0.001.

	n			r		separate	common slope	
	♂	♀	♂+♀	♂	♀	R^2-i	R^2-l	R^2-s
fraction lifted	98	90	-0.27 ***	-0.08	+0.24 *	0.02 *	0.00	0.10 *
handling time lifted	68	60	+0.27 **	+0.19	+0.11	0.00	0.02	0.00
handling time <i>in situ</i>	56	46	+0.09	-0.24	+0.16	0.00	0.04 *	0.04 *

Table 5. What are the effects of sex and bill tip width on parameters of handling *Macoma*? Each row provides the results for one parameter. Variance explained in an ANCOVA with separate slopes (R^2-i = interaction) and an ANCOVA with fixed common slope (R^2-w and R^2-s = bill tip width and sex). Stars indicate statistical significance: * p < 0.05, ** p < 0.01, *** p < 0.001.

	n			r		separate	common slope	
	♂	♀	♂+♀	♂	♀	R^2-i	R^2-w	R^2-s
fraction lifted	97	90	+0.09 -	0.03	+0.03	0%	0.00	0.17 ***
handling time lifted	67	60	+0.04 -	0.01	+0.29 *	5% *	0.01	0.07 *
handling time <i>in situ</i>	55	46	+0.02 -	0.09	+0.29	4%	0.00	0.00

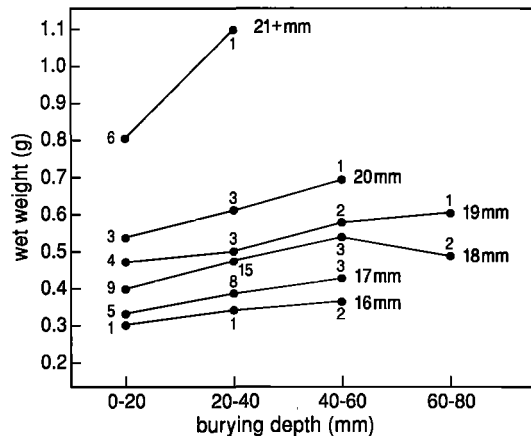


Fig. 7. The flesh content (fresh weight) of *Macoma* of different shell lengths in relation to burying depth. The *Macoma* were retrieved 24 hours after settling by slicing the sediment in layers of 2 cm thickness. Figures refer to the number of *Macoma* per depth class.

Bill length Although all *Macoma* were in reach of the bill for practically all of the ♂♂ (mean bill length 69.8, range 59-83 mm) and for all ♀♀ (mean 78.4, range 69-91 mm), bill length could still play a role in the choice between lifting or eating *in situ*. The bill exerts downward forces upon the shell, pushing it further into the sediment during opening as well as when the flesh is loosened. Possibly, both opening and cleaning the shell become more difficult the deeper the prey is buried. If so, the fraction lifted should increase with bill length and handling time *in situ* should increase with burying depth.

The captive ♂ and ♀ mainly opened shallow *Macoma in situ* and the deeper ones were lifted (Fig. 5A), supporting the hypothesis. But in the field data there is a significant and positive correlation between bill length and the fraction lifted for ♀♀, despite the fact that for ♂♂ and ♀♀ combined this correlation was negative, as expected (Table 4). The ANCOVA demonstrates that the interaction between sex and bill length is indeed significant (Table 4). However, if an ANCOVA with a fixed common slope is fitted, only

sex contributes significantly to the variance explained.

We cannot directly test whether handling time increases with depth, but the statistical analysis of the relationship between handling time (lifted or *in situ*), bill length and sex do not suggest this (Table 4).

Morphology of the bill tip A buried and undisturbed *Macoma* gapes slightly (Hulscher 1982). To open a *Macoma in situ*, the tip of the bill is inserted into the gape. Two features of the tip may be important: width and shape. We expect that it will be easier to penetrate into the shell with a thin tip than with a thick one and with a pointed tip rather than an intermediate or blunt tip. We thus expect that both the percentage of lifted *Macoma* and the handling time *in situ* are affected by either the width and/or the shape of the tip.

More ♂♂ have blunt and more ♀♀ have pointed bills, resulting on average in a larger tip width for the ♂♂ (Table 3). The covariance analysis of the percentages of lifted *Macoma* showed no significant effect of the bill tip width, but sex explained 17% (Table 5). A similar analysis of the handling times *in situ* revealed no significant effects, neither for the width of the bill tip, nor for sex; for the handling times of lifted *Macoma* thickness did not, but sex did contribute significantly to the total variance in a model with a fixed common slope. Thus, contrary to expectation, bill tip width does not seem to influence lifting or the time to handle *Macoma*, either *in situ* or when lifting.

The two-way ANOVA of the fraction of lifted *Macoma* showed no significant effect for shape, but it did for sex (Table 6). For the handling times *in situ*, neither shape nor sex contribute significantly to the total variance. For handling times of lifted *Macoma*, no influence of shape was again found, but sex contributed significantly (Table 6). We must conclude that the shape of the bill tip does not substantially influence the lifting behaviour nor the rate at which *Macoma* is handled. Nor does it account for the differences between the sexes.

lifted (Table 7, Fig. 8). Thus, we have no evidence that bill strength influences the tendency of individuals to lift *Macoma*.

DISCUSSION

Causes of the differences in handling between the sexes

♂♂ always lifted *Macoma* more than ♀♀ did (Fig. 3A). ♂♂ also handled lifted *Macoma* quicker than ♀♀ (in two of the three series), whereas the ♀♀ were quicker in handling *Macoma in situ* (in two of the three series, Fig. 3E). We failed to identify how these differences came about. It may be that the blunt bill tip of the ♂ is more appropriate to open *Macoma* by hammering than the pointed bill of the ♀. We probably can learn more by measuring the different components of handling (lifting, opening and cleaning) separately. Such a procedure has been followed by Wanink & Zwarts (1996) for Oystercatchers feeding on *Mya* and *Scrobicularia* in captivity. It may then be clear which sex is better at lifting, opening or cleaning *Macoma*, and which bill characteristics are involved in these acts. For a start, we may list what we know about these phases:

(1) Lifting phase: lifting itself takes some time, which is saved when *Macoma* is handled *in situ*.

(2) Opening phase: opening the closed shell of a lifted *Macoma* by hammering is more time consuming than opening a similar sized *Macoma in situ*, since the latter probably gapes wide enough to allow the bill tip to penetrate easily. But lifted *Macoma* are probably larger, although this is only documented for the captive birds (Table 2). A bigger size of the lifted *Macoma* in the field is plausible though, because the free-living birds just like the captives, extracted more meat from a lifted *Macoma* than one opened *in situ* (Fig. 3C). Opening a lifted *Macoma* by hammering not only takes more time because the shell is closed more tightly, but its larger size also requires an extra force to overcome the greater resistance of the larger adductors.

(3) Cleaning phase: cleaning the shell of a lifted *Macoma* also takes more time because it contains more flesh. Total handling times and shell length (meat volume), within and between species, are strongly positively correlated (Hulscher 1982 for *Macoma*, Meire & Ervynck 1986 for *Mytilus*, Wanink & Zwarts 1996 for *Mya* and *Scrobicularia*, Hulscher 1996 for different species). The meat content (M , mg AFDW) of *Macoma*, averaged over all burying depths, was calculated to relate to shell length (L , mm):

$$M = 0.028L^{2.789}.$$

Comparable data for *Macoma* are published by Zwarts (1991). Taking the sizes of the *Macoma* lifted and *in situ* by the captive birds (Table 2) into account, the calculated wet flesh weight of a lifted *Macoma* must have been 86.6 mg, and of one *in situ* 62.8 mg for the ♂ and 73.1 and 67.6 mg respectively for the ♀. The actual weight of lifted *Macoma* might have been greater, because lifted *Macoma* are found deeper than those *in situ* (Fig. 5A) and deeply buried *Macoma* are heavier (Fig. 7). The quantities of meat the birds extracted from the different categories of *Macoma* more or less matched the calculated quantities they should contain, so little flesh was left in the shells.

Consequences for search strategy

Even though we do not fully understand the differences that we noted between ♂♂ and ♀♀ in handling and capturing *Macoma*, they probably imply that differences in search strategy exist between the sexes. The captive ♂ and ♀ birds located the *Macoma* they subsequently lifted at a deeper depth than those they opened *in situ* (Fig. 5A). If this is also true in the field, it follows that ♂♂, which generally take to lifting *Macoma*, should search on average at a greater depth than ♀♀ do. In the field it took both sexes an equal amount of time to find an edible *Macoma* (Fig. 3B). This suggests that ♂♂ and ♀♀ use different selection criteria when looking for the bivalve. ♂♂ locate large, deeply buried *Macoma*, containing on average more meat than shallow ones (Fig.

Table 6. What are the effects of sex and bill tip shape on parameters of handling *Macoma*? Each row provides the results for one parameter. Two-way ANOVA (R^2-i = interaction, R^2-sh = shape, R^2-s = sex). Stars indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	<i>n</i>		two-way ANOVA		
	♂	♀	R^2-i	R^2-sh	R^2-s
fraction lifted	96	90	0.03 *	0.00	0.05 *
handling time lifted	66	59	0.01	0.01	0.03 *
handling time <i>in situ</i>	55	46	0.01	0.01	0.00

Table 7. What are the effects of sex and bill strength (bill height divided by bill length) on parameters of handling *Macoma*? Each row provides the results for one parameter. Variance explained in an ANCOVA with separate slopes (R^2-i = interaction) and an ANCOVA with fixed common slope (R^2-st and R^2-s = bill strength and sex). Stars indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	<i>n</i>			<i>r</i>		separate	common slope	
	♂	♀	♂+♀	♂	♀	R^2-i	R^2-st	R^2-s
fraction lifted	97	90	+0.35 ***	-0.05	+0.05	0.06	0.00	0.04 **
handling time lifted	67	60	-0.25 **	-0.14	-0.00	0.00	0.00	0.01
handling time <i>in situ</i>	55	46	-0.07	-0.28 *	-0.08	0.01	0.04 *	0.04 *

Bill strength The shorter, deeper and wider a bill is, the greater is its strength; hence ♂♂ have stronger bills than ♀♀. Probably as a result, ♂♂ more often feed on large sturdy prey, like Mussels, and are more likely to hammer their prey than ♀♀ (Hulscher & Ens 1992, Durell *et al.* 1993). Lifted *Macoma* are always opened by hammering. Possibly, therefore, Oystercatchers with stronger bills are inclined to open *Macoma* more by hammering and hence to lift them. We tested this hypothesis by taking the ratio bill depth/bill length as an index for strength, i.e. low values correspond to weak bills. The results closely mirror those for bill length (compare Table 7 to Table 4), with one important exception: when the effect of bill strength is taken out, sex explains much less of the remaining variance (only 4%) than when the effect of bill length is taken out (10%). This is due to the fact that bill strength correlates more closely with sex than bill length does. None-

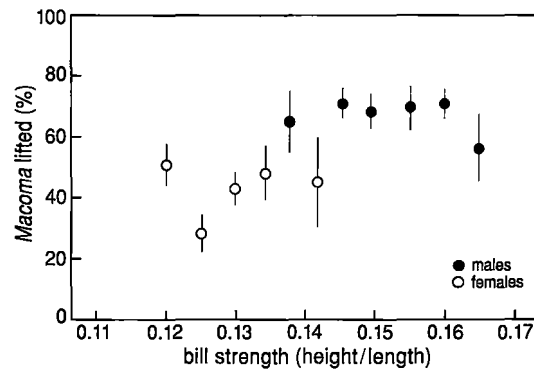


Fig. 8. Plot of the fraction of lifted *Macoma* (arcsine transformed) against the strength of the bill (defined as the ratio of bill depth divided by bill length). Each dot represents the mean value for approximately 20 individuals, while bars represent 1 SE.

theless, this 4% is still significant and within a sex bill strength does not correlate with the fraction

7 and Zwarts & Wanink 1991), and they open them by hammering. ♀♀ locate shallow, gaping *Macoma* and continue to open them *in situ*. On the one hand, searching at a smaller depth may imply that the deeper *Macoma* remain undetected, reducing the available density of *Macoma*. On the other hand, shallow searching may afford a higher searching rate, enhancing the number of prey encountered. Of the two captive birds the ♀ was the quickest in finding *Macoma*, as expected (Table 2).

Conclusion

The fact that we could not identify a morphological character of the bill that predicts the handling of *Macoma* better than the sex of the bird hints at the intriguing possibility that both searching for and handling this bivalve are primarily determined by its sex, irrespective of the morphology of its bill. However, the data are quite variable, possibly due to the large variation in feeding conditions. Ideally, a great number of individuals varying in sex and bill morphology should be tested under standard conditions to settle the matter.

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SAMENVATTING

Scholeksters eten vooral tweekleppige schelpdieren, die zij met hun sterke, platte snavels open maken, waarmee zij vervolgens het vlees losmaken en opeten. Onder de schelpdieren vormt het Nonnetje *Macoma balthica* een belangrijk aandeel van het menu van Scholeksters, vooral in de zomer. Voor Scholeksters is het Nonnetje een kleine prooi met een schelpenlengte van 10-24 mm, dat ingegraven in de wadbodem leeft, de meeste 's zomers niet dieper dan 2 tot 4 cm. Mannelijke en vrouwelijke Scholeksters verschillen in snavelbouw. De ♂♂ hebben vooral korte, hoge en iets bredere, de vrouwtjes lange en dunne snavels. Verder is het uiterste topje van de snavel, van opzij bekeken, bij ♂♂ vaker recht afgesneden (stomp), bij ♀♀ vaker puntig. Wij willen nu weten of de verschillen in snavelbouw tot uitdrukking komen bij de manier waarop de beide sexen Nonnetjes behandelen bij het openmaken en leegeten

van de schelp. Waarnemingen werden gedaan in de Waddenzee, bij Paesens aan de Friese kust en op Schiermonnikoog. Er werd uitsluitend gekeken naar volwassen, door kleuringen individueel herkenbare Scholeksters, waarvan het geslacht en de snavelbouw bekend was. Verder werden aanvullende waarnemingen gedaan aan twee gevangen Scholeksters, een ♂ en een ♀, die in een grote kooi bakken met wadmodder kregen aangeboden, waarin Nonnetjes van bekende grootte waren ingegraven. Het blijkt dat de voedselopname, dat is de hoeveelheid vlees die de vogels per tijdseenheid voedselzoeken naar binnen werken, voor ♂♂ en ♀♀ niet verschilt, maar dat dit resultaat op een verschillende manier tot stand komt. ♂♂ graven Nonnetjes vaker op en leggen deze op het oppervlak neer alvorens de schelp te openen (liften genoemd), ♀♀ eten de Nonnetjes vaker ondergronds leeg (*in situ* eten genoemd). Beide sexen hanteren een *in situ* Nonnetje sneller dan een gelift Nonnetje. Het tijdverlies voor de ♂♂, omdat zij vaker een Nonnetje liften, wordt gecompenseerd door de grotere Nonnetjes die zij bij het liften vinden en die meer vlees bevatten dan de kleinere, *in situ* gevonden Nonnetjes. De tijd die de vogels nodig hebben om een eetbaar Nonnetje te vinden verschilt gemiddeld niet voor de geslachten, met als uiteindelijk resultaat dat er geen verschil is in de opname van ♂♂ en ♀♀. Is het nu mogelijk deze verschillen tussen de sexen in de mate waarin Nonnetjes worden gelift en de tijd waarin deze gelifte Nonnetjes worden gehanteerd in verband te brengen met de verschillen in snavelbouw? Merkwaardig genoeg niet. Er is namelijk geen enkele snavelmaat die binnen een sexe het verband vertoont dat overeenkomt met het verschil tussen de sexen.